

# Effect of drought on plant physiology, disease susceptibility and insect herbivory in rainforest tree saplings

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## Abstract

Two rainforest canopy tree species were sampled as saplings in June 2022 in a cross-sectional study to compare the effect of drought on physiological performance, insect herbivory and leaf disease damage. Throughfall infrastructure was utilised to simulate drought in field conditions. A strong effect of drought was found across all physiological measures, with drought being correlated with lower leaf chlorophyll content, stomatal conductance and photosystem 2 efficiency. Plant health was assessed at the leaf level using a 0–5 visual scale. No significant effect of drought on insect herbivory or disease damage was found, except in *Argyrodendron peralatum*. Correlation of physiological performance and individual health assessments revealed several trends in susceptibility. Chlorophyll content was found to be more steeply correlated to insect damage severity in drought treatments than in control treatments, the effect of stomatal water conductance was investigated, and reduction in efficiency of photosystem 2 was correlated to higher severity of affliction. Mechanisms behind trends in susceptibility were investigated, but the inference power of this study was limited by its cross-sectional nature. A longitudinal study tracking the progression of plant health metrics, physiological performance and development is suggested for future research in conjunction with studies that analyse drought impact on invertebrate communities.

**Running Title:** Disease susceptibility and insect herbivory in rainforest saplings

**Key Words:** Natural ecosystems, severity, pathogens, throughfall, rainfall exclusion

## Introduction

In natural forest ecosystems, pathogens and insects function as primary consumers that shape community structure and ecosystem processes through their impacts on tree mortality, decomposition and physiology (Cobb & Metz 2017; Franklin *et al.* 1987; Mordecai 2011; Preston *et al.* 2016; Semler-Williamson *et al.* 2019). Insects, pathogens and nematodes comprise the most abundant and species-rich organisms in forest ecosystems, with insect herbivores having been found to consume four to five times more plant material than vertebrate species (Coley & Barone 1996; Stork *et al.* 2015). It has been hypothesised that pathogens and herbivores – these natural enemies of plant species – play a crucial role

Grishin *et al.*: Disease susceptibility and insect herbivory in droughted rainforest saplings

in creating and maintaining high biodiversity in tropical rainforests through elevated mortality acting heterogeneously across the environment (Bagchi *et al.* 2014). Under the effects of climate change, droughts are expected to increase in frequency and severity, altering the dynamics of plant–insect interactions in highly variable ways (Gely *et al.* 2020; Sconiers *et al.* 2020). Given the multiple interacting environmental stresses that plants face under climate change, the responses of forest ecosystems to changing drought conditions could have important implications for agricultural and natural systems (Niinemets 2010).

Drought frequency and severity affect plant physiology, altering pathogen and herbivore response as photosynthesis, water use and nutrient content co-vary with natural enemy predation and environmental stress factors (Sconiers *et al.* 2020). The growth-differentiation balance hypothesis suggests a trade-off in plant resource allocation to growth, defence or other physiological processes according to stress or resource availability (Herms & Mattson 1992). Thus, under drought stress conditions, investment and development of non-structural carbohydrates into secondary defence metabolites is likely to be down-regulated, increasing host susceptibility (Herms & Mattson 1992). Notably, under increasing drought severity, photosynthesis and stomatal conductance decrease, while chlorophyll content increases (Sconiers *et al.* 2020). Moderate drought conditions stimulate higher concentrations of carbon and nitrogen within tree tissues, whereas under severe drought most investment is down-regulated as plants become increasingly water- and carbon-stressed, resulting in more palatable and less toxic tissues, which increases susceptibility to natural enemies (Farooq *et al.* 2009; Gely *et al.* 2020).

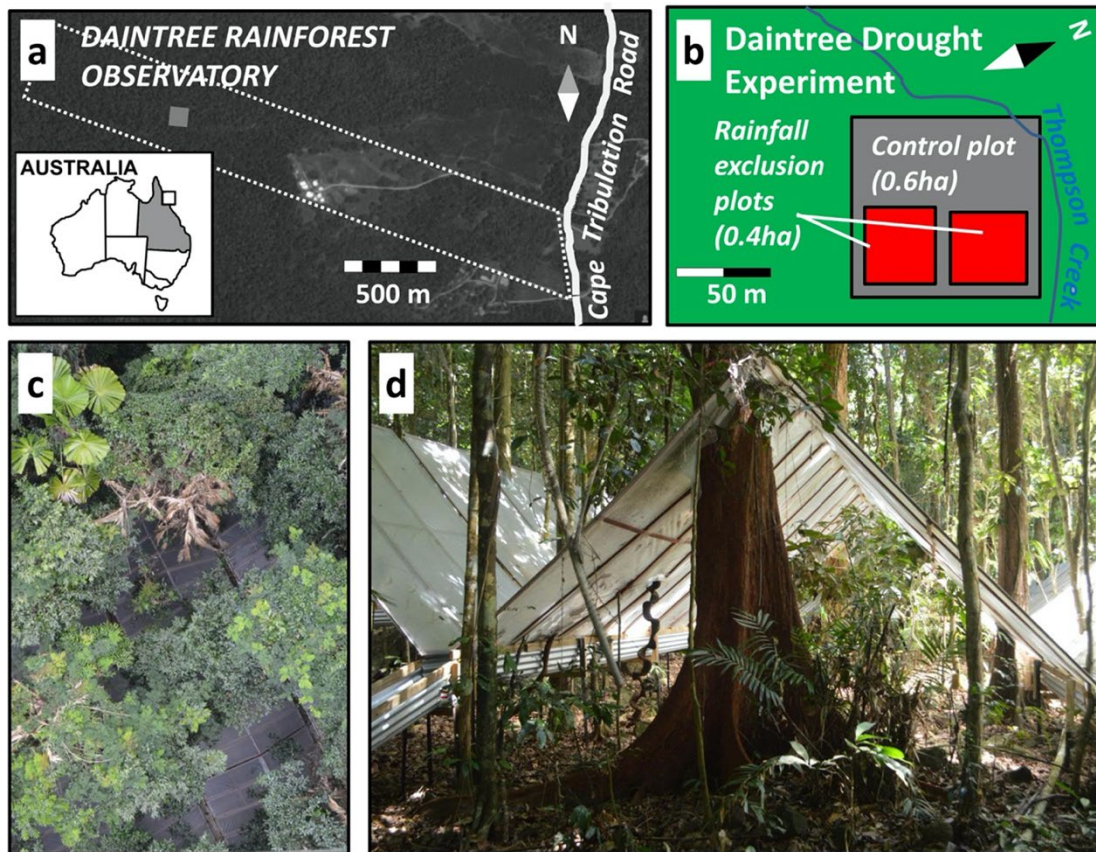
Most field studies in tropical rainforest to date have focused on the susceptibility of mature trees (Meir, Mencuccini *et al.* 2015; Schuldt *et al.* 2011); however, tree saplings are crucial to the continual recruitment of forest stands, allowing the perpetuation of diversity and associated vegetation dynamics (Royo & Carson 2006; Poorter & Markesteijn 2008). The general understanding is that tree saplings are more susceptible to single stresses such as drought, herbivory and pathogens due to undeveloped concentrations of plant defence chemicals as well as shallow roots (Niinemets 2010; Tng *et al.* 2022); however, few studies have tested these assumptions in multi-stress environments in the field.

Rainfall exclusion or throughfall infrastructure is one way to test the effects of drought on forest stands *in situ* (Meir, Wood *et al.* 2015; Rowland *et al.* 2015). This study utilises the throughfall infrastructure of the Daintree Rainforest Observatory (DRO), established in 2015 for use in the Daintree Drought Experiment (Laurance 2015; Tng *et al.* 2022). In 2015, after six months of simulated drought conditions at the DRO, Tng *et al.* (2022) analysed the effects of drought on sapling physiological performance and susceptibility to disease and insect herbivory, and found a strong negative effect of drought on performance, disease symptoms and herbivory. Using similar techniques to Tng *et al.* (2022), this study aims to: (1) confirm whether physiological drought responses are still evident in drought treatment plants; (2) analyse the progression of plant health in terms of severity of affliction by disease and herbivory after seven years of rainfall exclusion at the DRO; and, to further the previous work, (3) correlate leaf trait physiological performance measures with individual plant health assessments to reveal trends in susceptibility. On the basis of Tng *et al.*'s (2022) findings, we hypothesise that saplings subjected to the drought treatment will demonstrate signs of physiological drought stress as well as higher affliction by herbivory and disease than non-drought plants.

## Methods

### *Overview*

Our study site was located at the DRO (16°06'20''S 145°26'40''E, 50 m ASL) in a lowland rainforest adjacent to the Daintree National Park in Cape Tribulation, Far North Queensland (Figure 1). This region receives an average rainfall of 4,900 mm year<sup>-1</sup> and a mean temperature of 24.4 °C (Bureau of Meteorology 2022). The soils are formed over metamorphic and granitic colluvium and are highly fertile (Bass *et al.* 2011).



**Figure 1:** (a) study location in the Daintree Rainforest Observatory, Cape Tribulation, Far North Queensland; (b) schematic of experimental plot; (c) top-down view of rainfall exclusion infrastructure; (d) cross-section of the throughfall infrastructure. Source: Tng *et al.* (2020).

### Sample environment

In May 2015, a throughfall rain exclusion experiment began with the erection of clear-panel roofing structures over 0.4 ha of the 1-ha experimental plot (Tng *et al.* 2022). The roofing panels were installed between rows of elevated aluminium gutters. The height of the enclosures is 2.8 m, completely covering all saplings and allowing taller stems to emerge through the clear panels. The drought plots are designed to reduce overall rainfall by 30% (Laurance 2015).

### Sampling protocol

In June 2022, two canopy tree species within drought and control plots at the DRO underwent comparative physiology and susceptibility analyses. Overall, 28 individuals were sampled, with 14 per species and 14 per treatment (Table 1). We selected two target species based on quantity of replicates found within the 1-ha experimental plot and representation of different canopy strata: *Argyrodendron peralatum* (Malvaceae) and *Myristica globosa* subsp. *muelleri* (Myristicaceae), both commonly found in the Daintree Rainforest. We performed susceptibility and physiological performance assessments of the sample saplings using several non-destructive methods, namely, (i) qualitative visual assessments of disease presence and damage, and signs of insect herbivory, and (ii) physiological performance measures.

Grishin *et al.*: Disease susceptibility and insect herbivory in droughted rainforest saplings

**Table 1:** Number of replicates of each species sampled within the drought and control treatments for severity of pathogen and herbivory damage as well as physiological performance measures after seven years of simulated drought conditions in a throughfall experiment at the Daintree Rainforest Observatory, Cape Tribulation, Far North Queensland.

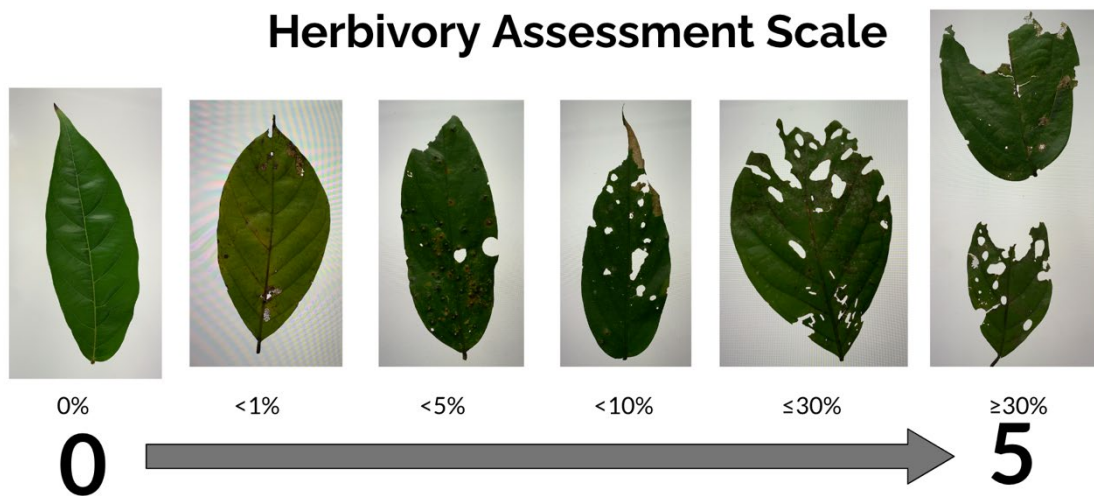
Species	Family	Control (n)	Drought (n)
<i>Argyrodendron peralatum</i>	Malvaceae	7	7
<i>Myristica globosa</i>	Myristicaceae	7	7

### *Qualitative damage assessment*

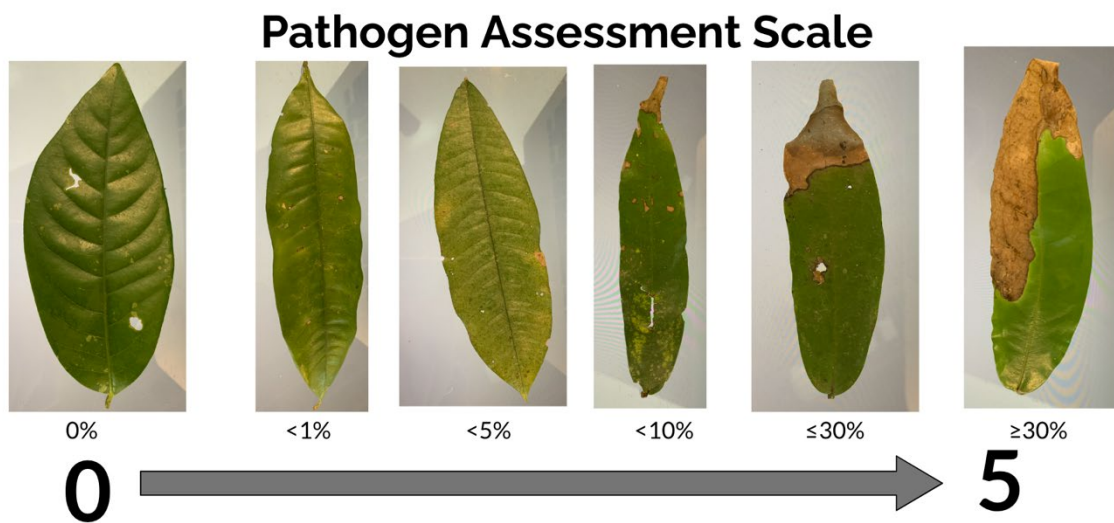
To attain an accurate representation of plant health, a visual scoring system was created for both pathogen damage and insect damage in drought and control plots. The scoring system assessed damage at the leaf level, based on percentage coverage estimated using the herbivory-measuring app LeafByte (LeafByte 2022). A 0–5 visual scoring system was created to represent the spread of damage found in experimental conditions that was able to be determined by an observer (Figures 2 & 3). This scoring system was then applied to ten intermediately aged leaves of each species replicated by two independent observers, creating a single average score for a single plant. Insect herbivory was defined as holes or patches with sharp non-necrotic edges; pathogen and disease damage was defined as patches or spots with yellow, white or dark discolouration, leaf necrosis, or chlorosis. Both top and bottom surfaces were inspected for insect or pathogen damage.

### *Physiological performance measures*

The physiological performance assessment was performed using three measures on each individual: stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ) was measured using a Li-600 porometer/fluorometer; chlorophyll content (SPAD units) was compared within species using a SPAD chlorophyll meter; and photosynthetic capacity was estimated using quantum yield of fluorescence ( $\Phi_{PSII}$ ) measured via a Li-600 porometer/fluorometer. All physiological measures were conducted between 10:00 am and 03:00 pm.



**Figure 2:** Visual guide to insect herbivory damage categories.



**Figure 3:** Visual guide to pathogen damage categories.

#### *Understorey microclimate*

Due to algal growth on the clear panels, the roofing structures designed to reduce rainfall also effect the amount of incidence sunlight, altering the microclimate beneath them. To help account for this variation, solar radiation flux density ( $\text{mol m}^{-2}\text{s}^{-1}$ ) was measured using a photosynthetically active radiation (PAR) flux meter (measuring the wavelength range from 400 nm to 700 nm) at every plant, constituting 28 individual observations. Furthermore, the presence of drought was verified through testing of topsoil moisture content (%) at every plant via the use of a soil moisture probe.

#### *Data analysis*

Grishin *et al.*: Disease susceptibility and insect herbivory in droughted rainforest saplings



Pertaining to the first aim of this experiment, the means of plant chlorophyll content, stomatal conductance and chlorophyll fluorescence were calculated and compared between control and drought treatment plots using one-tailed t-tests in RStudio (RStudio Team 2022). Abiotic conditions such as light levels and soil moisture were aggregated across both species and their means compared using one-tailed t-tests ( $\alpha = 0.05$ ). One-tailed tests were employed due to the study's paired design methodology as well as *a priori* directional hypotheses, in line with analyses conducted by Tng *et al.* (2022).

Pertaining to the second aim, leaf-level observations from both observers were aggregated to form an average damage score for each individual plant. These scores were then pooled within treatments and species to form a by-species comparison of drought impact on insect herbivory and pathogen damage. Significance testing was conducted using zero-inflated generalised linear models (poisson, categorical) in R.

Pertaining to the third aim, individual-level data were used to plot linear models of physiological responses to herbivory and pathogen scores using the *statsmooth* method in RStudio 13. Trends were analysed qualitatively; however, differences between slopes will be included in future analyses.

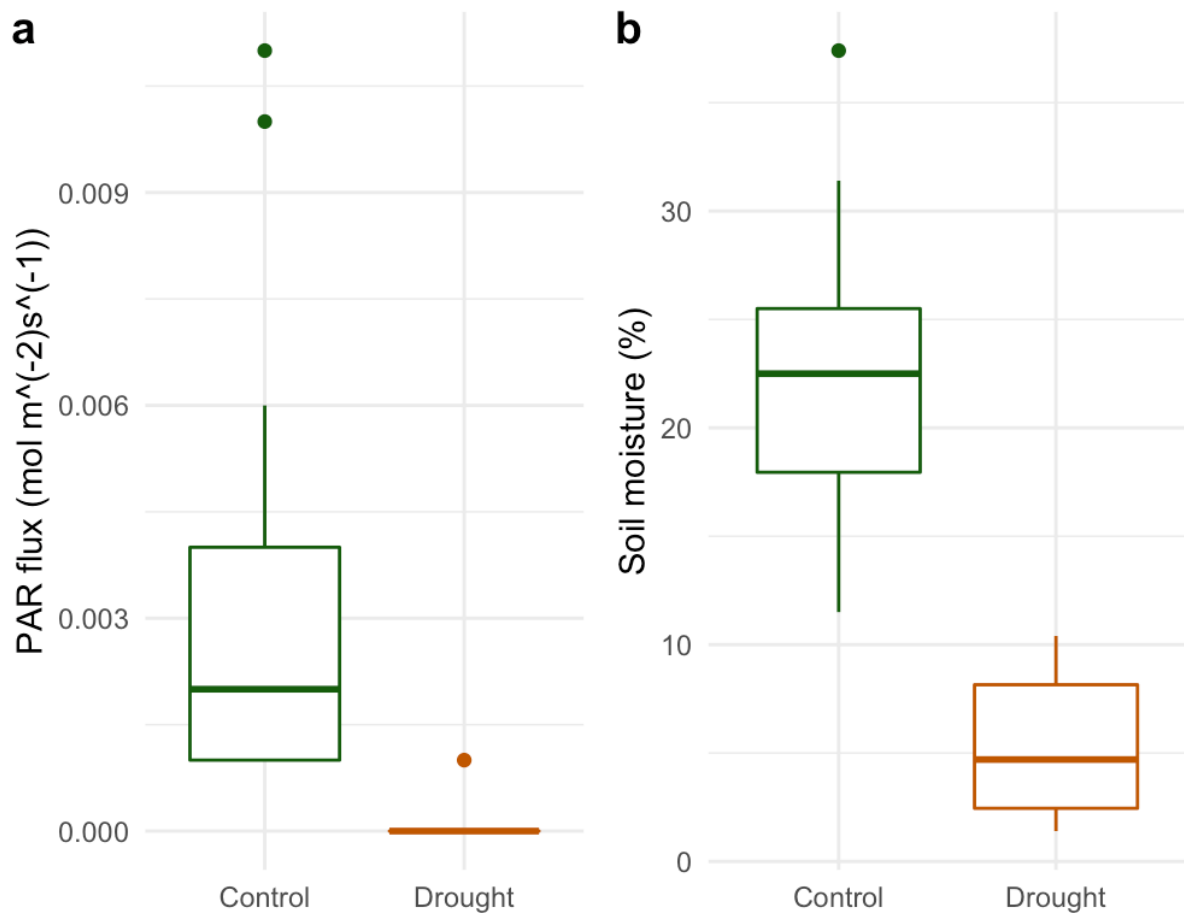
## Results

### *Abiotic conditions*

Light levels in the drought plots were significantly lower than in the control plots (Figure 4; Table 2). Similarly, soil moisture content was significantly lower in drought plots than in control plots (Table 2).

**Table 2:** Summary of abiotic conditions in drought and control plots.

	Light $mol\ m^{-2}\ s^{-1}$	Soil moisture %
Control	$3.6 \times 10^{-3} \pm 3.4 \times 10^{-2}$	$22.7 \pm 7.33$
Drought	$7 \times 10^{-5} \pm 2.6 \times 10^{-3}$	$5.26 \pm 3.31$
P-value	$P < 0.001$	$P < 0.001$



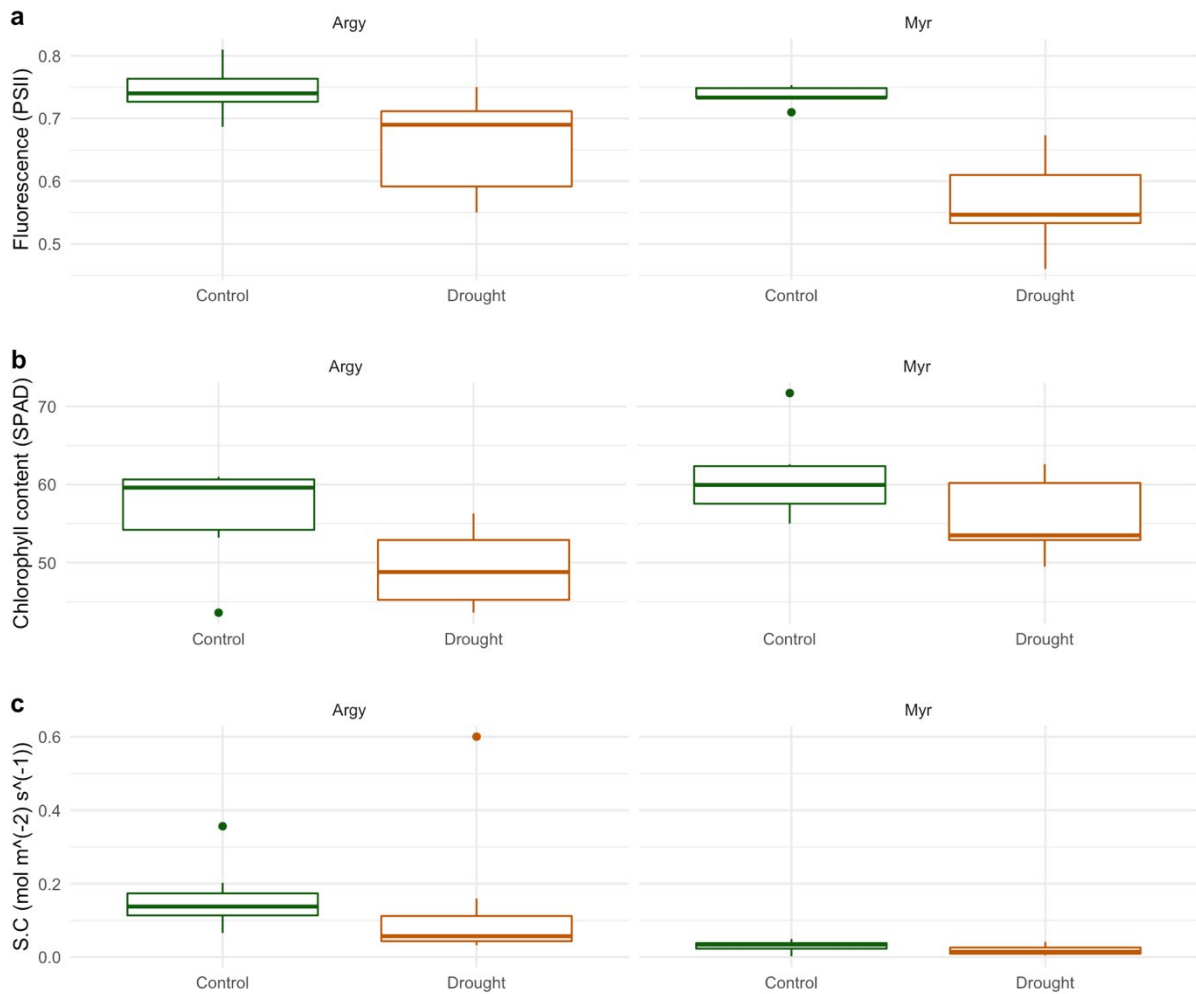
**Figure 4:** Boxplots of (a) PAR flux density in control and drought treatments, and (b) soil moisture % in control and drought treatments.

### Physiological performance

All physiological performance measures were found to be significantly lower in drought treatment plots than in control plots (Table 3, Figure 5).

**Table 3:** Summary of physiological performance measures in drought and control plots. P-values represent difference between treatments. Between-species P-values are not presented.

	Fluorescence ( $\psi_{PSII}$ )	Stomatal conductance ( $\text{mol m}^{-2}\text{s}^{-1}$ )	Chlorophyll content (SPAD)
Control			
- <i>A. peralatum</i>	$0.745 \pm 0.041$	$0.162 \pm 0.096$	$56.3 \pm 6.37$
- <i>M. globosa</i> subsp. <i>muelleri</i>	$0.736 \pm 0.016$	$0.030 \pm 0.017$	$61.1 \pm 5.91$
Drought			
- <i>A. peralatum</i>	$0.657 \pm 0.79$	$0.066 \pm 0.043$	$49.3 \pm 4.84$
- <i>M. globosa</i> subsp. <i>muelleri</i>	$0.567 \pm 0.075$	$0.013 \pm 0.020$	$56 \pm 5.03$
P-value	$P < 0.001$	$P = 0.016$	$P = 0.008$

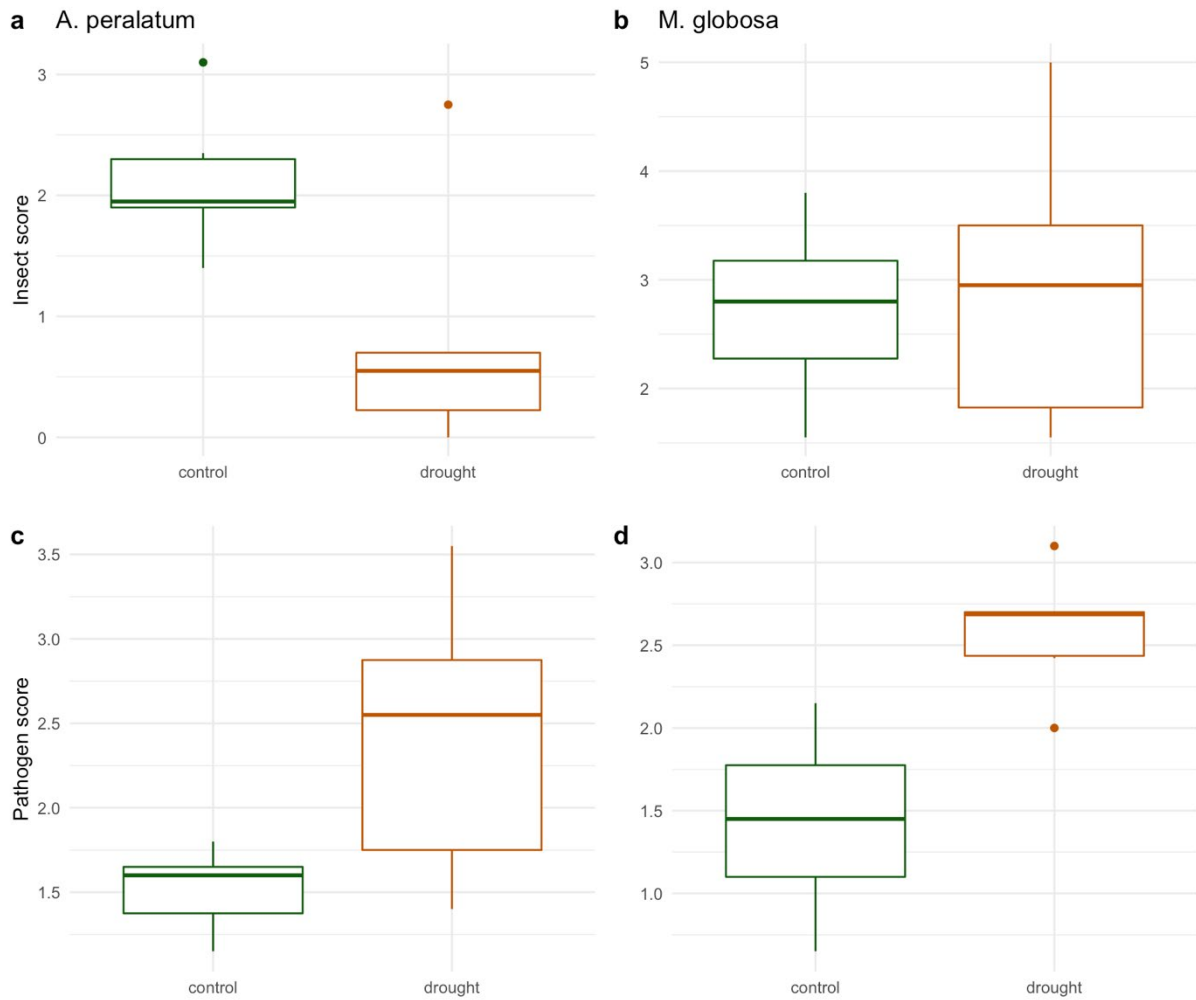


**Figure 5:** Boxplots of (a) chlorophyll Fluorescence as measured by a handheld Li-COR between drought and control treatments by species. (b) Chlorophyll content in drought and control treatments by species. (c) Stomatal conductance in drought and control treatments by species. Argy is *A. peralatum* and Myr is *M. globosa subsp. muelleri*.

### Visual plant health assessments

Overall, no significant trend was found in plant health assessments between drought and control treatments (Table 4, Figure 6).





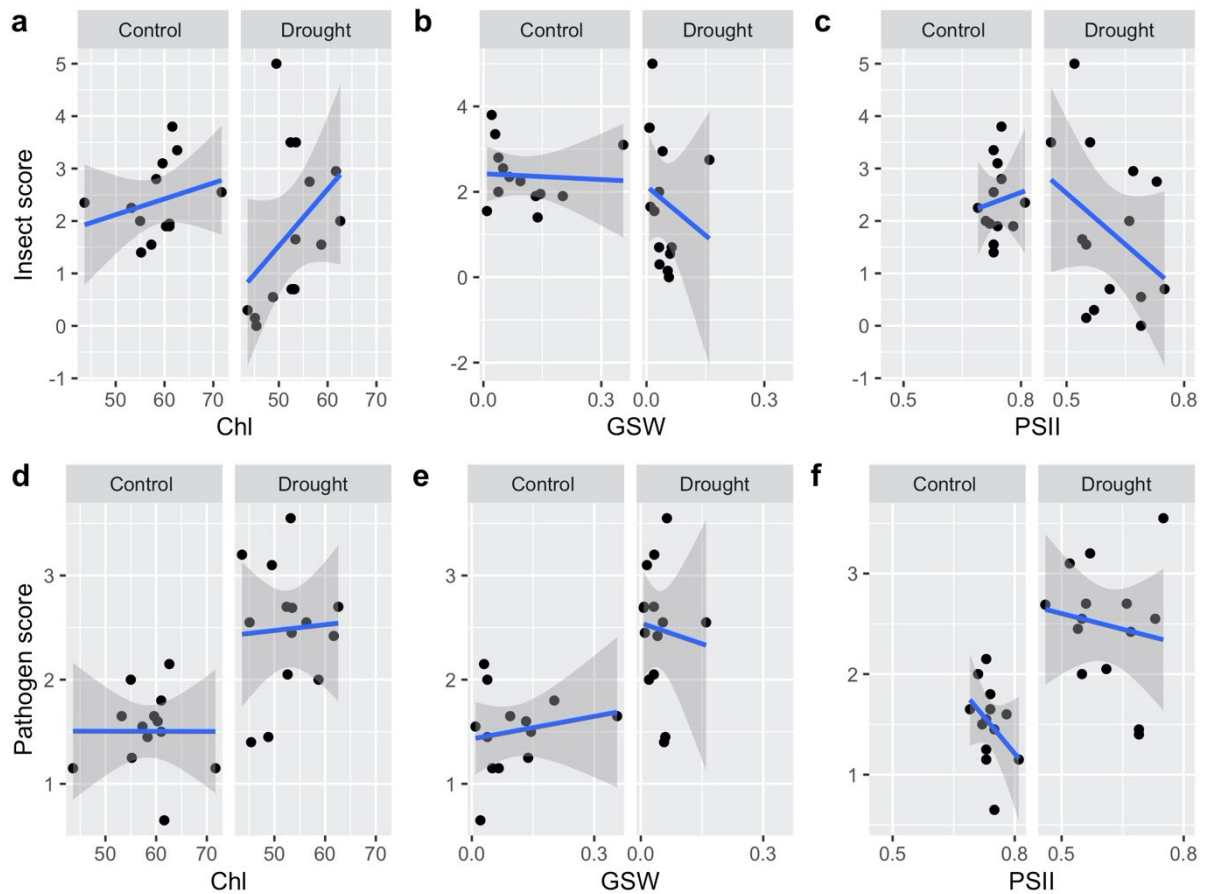
**Figure 6:** Boxplots of damage severity assessments for (a) *A. peralatum* insect damage ( $p = 0.038$ ), (c) *A. peralatum* pathogen damage ( $p = ns$ ), (b) *M. globosa* subsp. *muelleri* insect damage ( $p = ns$ ), (d) *M. globosa* subsp. *muelleri* pathogen damage ( $p = ns$ ). Data collected at the Daintree Rainforest Observatory, Cape Tribulation, Australia.

**Table 4:** Summary of plant health assessments in drought and control plots. P-values represent differences within species.

	Insect score	Pathogen score
Control		
- <i>A. peralatum</i>	2.12 ± 0.53	1.51 ± 0.23
- <i>M. globosa</i> subsp. <i>muelleri</i>	2.72 ± 0.77	1.43 ± 0.53
Drought		
- <i>A. peralatum</i>	0.74 ± 0.93	2.39 ± 0.82
- <i>M. globosa</i> subsp. <i>muelleri</i>	2.88 ± 1.25	2.58 ± 0.34
P-value		
- <i>A. peralatum</i>	p = 0.038	p = ns
- <i>M. globosa</i> subsp. <i>muelleri</i>	p = ns	p = ns

#### *Trends in susceptibility*

Trends in susceptibility across both species are shown in terms of regression of health measures to physiological performance measures. Generally, greater susceptibility is demonstrated when a steeper slope is observed: a plant will have a faster degradation of health (Figure 10). Chlorophyll content and insect score showed a steeper positive slope under drought conditions than control conditions (Figure 10a). Stomatal conductance demonstrated no strong response to insect damage score in control conditions, but in drought conditions a negative slope was found (Figure 10b). Quantum yield of PSII demonstrated a positive slope in response to insect score under control conditions, but this slope was found to be negative under drought conditions (Figure 10c). In terms of pathogen score, chlorophyll content showed no strong response in either control or drought treatments (Figure 10d). Stomatal conductance showed a slight positive response to pathogen score in control conditions, and a slight negative correlation to stomatal conductance under drought conditions (Figure 10e). PSII demonstrated a steep negative correlation to pathogen score in control treatments and a less negative correlation under drought conditions (Figure 10f).



**Figure 10:** Linear model correlation plots of physiological performance measures against individual sample health assessed by independent pathogen and insect scores. Chl signifies chlorophyll content (SPAD), GSW signifies stomatal water conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ), and PSII signifies quantum yield of PSII.

## Discussion

We aimed to: (1) confirm the presence of physiological drought responses in drought treatment plants as a baseline to interpreting our results; (2) analyse the progression of plant health in terms of severity of affliction by disease and herbivory after seven years of rainfall exclusion at the DRO; and (3) correlate physiological performance measures with individual plant health assessments to reveal trends in susceptibility. Two rainforest canopy tree species were sampled as saplings in June 2022. The effect of drought on insect herbivory and pathogen prevalence was assessed on a per-leaf basis to extrapolate plant health. Drought was simulated by a throughfall infrastructure established at the DRO in May 2015, excluding approximately 30% of rainfall. Seven years later, the presence of topsoil desiccation due to rainfall exclusion was confirmed with control plots averaging 22.7% soil moisture while drought plots averaged 5.26% ( $p < 0.001$ , Figure 5). This study follows on from a study conducted by Tng *et al* (2022) in November 2015, six months after the establishment of the drought plots at the DRO. Overall, this study found that while physiological performance measures such as chlorophyll fluorescence, stomatal conductance and chlorophyll content were indeed higher in control plots, this did not correlate to an increased presence of insect or pathogen damage.

This study acknowledges that throughfall infrastructure fails to capture the full suite of environmental changes that co-occur with drought, such as increased temperatures, reduced humidity and decreased vapour pressure deficit. The infrastructure also has significant impacts on the amount of light reaching the understorey, having been found to decrease light levels in drought plots by  $\sim 98\%$  ( $p < 0.001$ , Figure 4). Although not assessed

Grishin *et al.*: Disease susceptibility and insect herbivory in droughted rainforest saplings

in this study, the infrastructure also reduced the amount of fresh leaf litter in drought plots compared to control plots, possibly affecting invertebrate and fungal communities.

### *Presence of physiological drought stress*

Signs of physiological drought stress were evident in sample plants. In particular, chlorophyll content, stomatal conductance and photosynthesis in terms of chlorophyll fluorescence were found to be lower in drought treatment plants than in control treatment plants (Figures 6, 7 & 8) (Tng *et al.* 2022; Zhuang *et al.* 2020; Singh & Reddy 2011). These responses have been extensively studied in single stress studies in agricultural crops, revealing a strong correspondence of drought-induced photosynthetic inhibition and reduction in stomatal water conductance (Flexas & Medrano 2002). Changes in chlorophyll content have also been associated with drought stress due to varying allocation of nitrogen; in particular, wheat and barley have been found to have lower chlorophyll content after being exposed to drought conditions (Nikolaeva *et al.* 2010; Li *et al.* 2006). Conversely, the reduction in photosynthesis (Figure 8) could be due to foliar disease and insect attacks, as patches of leaf lamina that are afflicted may not be photosynthesising at their optimal rate due to damage to the vascular leaf tissue (Aldea *et al.* 2006; Tng *et al.* 2022).

### *Assessing severity of affliction between treatments*

The assessment of plant health in terms of severity of affliction by disease or insect herbivory revealed mostly non-significant differences between drought and control plots (Figure 9), except for insect herbivory of *A. peralatum*, which was found to be greater in control plots (Figure 9a). Interestingly, this contradicts the earlier findings of Tng *et al.* (2022), who found no significant increase in herbivory of disease affliction of *A. peralatum* in drought plots compared to control plots and found sharp increases in herbivory and disease affliction of *M. globosa*. Various reasons for this contradiction seem possible – namely, changed microclimate conditions relating to quantity and quality of leaf litter after seven years of rainfall exclusion (Peguero *et al.* 2019), an effect of survivorship bias in drought treatments, or the long-term impacts of water stress on leaf nutritional quality and structural qualities impacting palatability (Simler-Williamson *et al.* 2019). A 1996 study comparing the effects of leaf litter on relative growth rates, as well as insect and pathogen damage of a rainforest sapling, found that increased leaf litter positively corresponded with increased affliction over a one-year period (García-Guzmán & Benítez-Malvido 2003). Similarly, the long-term effect of rainfall exclusion infrastructure on reducing leaf litter accumulation could be the factor contributing to increased insect herbivory of *A. peralatum* in control plots where much greater leaf litter was observed (Figure 9a). Another possible reason for the contradiction could be differences in methodology between this study and the previous study, where this study used leaf-level assessments of damage severity to indicate overall plant health while the previous study employed an overall plant health metric by assessing total percentage of leaves afflicted by herbivory or disease. We believe that future research assessing plant health in terms of affliction by disease or herbivory should utilise methodology that factors in leaf-level damage severity rather than percentage of total leaves with damage present, as this can be more favourably combined with physiological and functional measures to reveal host plant responses at varying severity levels (Inglese & Paul 2007; Walters 2011; Grossman *et al.* 2019).

### *Trends in susceptibility*

Due to this study's temporal limitations, it could not account for the negative impact of natural enemies on the physiological performance of plants over time (Kerchev *et al.* 2012; Kessler & Baldwin 2002); nor could it explore the possibility that physiological drought responses are leading to increased susceptibility of plants (Gely *et al.* 2020). By correlating physiological performance to individual plant health assessments (Figure 10), we found the response of insect damage severity and chlorophyll content (Figure 10a) to be steeper in

Grishin *et al.*: Disease susceptibility and insect herbivory in droughted rainforest saplings

drought plots than in control plots, suggesting a higher susceptibility to insect herbivory under drought versus control conditions. This increased susceptibility may be due to lower carbon assimilation due to water stress and stomatal closure, decreasing the production of secondary metabolites used for chemical defence (Sconiers *et al.* 2020). The insect damage severity response of stomatal conductance demonstrated a slight negative correlation in control plots, suggesting a small decrease in severity as stomatal conductance increases, and a stronger negative correlation in drought plots, indicating a higher decrease in severity per unit of stomatal conductance increase (Figure 10b). Broadly, lower PSII operating efficiency was correlated with increased susceptibility to natural enemies (Figures 10c, 10f). In particular, plants in control plots interacted more steeply with pathogen damage severity than plants in drought plots (Figure 10f), suggesting that increased water availability may help regulate plant defence chemicals so that equally well-functioning plants in terms of PSII are less severely afflicted in control plots than in drought plots. However, this is not necessarily confirmed by stomatal conductance, which was demonstrated as being correlated with increasing pathogen damage severity in control plots and decreasing severity in drought plots (Figure 10e). However, this may be due to the fact that as plants became more physiologically impaired, insect herbivory targeted healthier plants with higher nitrogen content. Temporal scale seems critical here, because the slight positive correlation in control treatment of insect damage severity against PSII (Figure 10c) may suggest that insects initially favour healthy individuals. Thus, the affliction would stimulate decreases in physiological traits rather than vice versa.

Overall, the literature supports the finding that increasing PSII efficiency decreases the severity of affliction by natural enemies through the correlation of increased PSII with increased plant physiological function (Gely *et al.* 2020; Sconiers *et al.* 2020). All physiological performance measures declined in drought plots (Figures 6, 7, 8), and drought had no significant impact on insect herbivory or plant pathogen damage (Figure 9). This suggests that the measures used in this study are not strongly correlated to increased susceptibility of plants to affliction, and that other, possibly microclimatic or nutrient content-related, factors are at play. A thorough investigation of this question would require a longitudinal study that correlates ongoing plant health assessments and physiological performance measures at the individual level to converge on any cause–effect relationships. Future studies could incorporate tracking of leaf carbon:nitrogen ratios and microclimatic variables to enable more significant inference for causal mechanisms that are at play when insect herbivory or pathogen severity changes at the ecosystem level.

## Conclusions

Examining multiple responses in rainforest canopy tree saplings, we found that simulated drought via throughfall infrastructure caused a decrease in plant physiological performance; however, we found no strong effect on comparative plant health in terms of insect herbivory or disease damage. Our analyses of trends in correlation of individual plant health and physiological performance measures revealed that plant affliction by natural enemies and physiology may act synergistically to further decrease physiological performance and increase mortality over time; however, this study was limited to a single point in time. Our results have implications for the development of methodologies for the assessment of plant health and knowledge about the impacts of drought on plant health.

## Acknowledgements

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